Bioinvasions in fresh waters and the Nero dilemma.

POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	54	4	549–561	2006

State-of-the-art review

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BIOINVASIONS IN FRESH WATERS AND THE NERO DILEMMA

ABSTRACT: Human-mediated invasions of organisms are causing great harm to the environment, indigenous species, national economies, and human health. Notwithstanding Elton's (1958) prophecies, only by the mid 1980s did the negative impact of several introduced species become clear, along with the urgency to reduce the pace of bioinvasions. Often conservation biologists are faced with the Nero dilemma. Should they keep "fiddling" with their elegant experiments while biota are burning, or rather act, even before achieving a "strong verification" of their hypotheses? Indeed, we do need a comprehensive scientific understanding of the biological features, ecological effects, and spread potential of invasive species in order to be able to improve our strategies for mitigating their impacts. Abundant data have been collected during the past two decades on a growing number of case studies. The theories on bioinvasions derived from that wealth of knowledge have indeed revealed their predictive power. We should now strive towards a quick transfer of this knowledge from the laboratories to the "real world".

KEY WORDS: biological invasions, management, biodiversity conservation, fresh waters

1. INTRODUCTION

In 1958, Charles Elton predicted "huge changes in the natural populations balance of the world", changes that would have led to "one of the great historical convulsions in the world's fauna and flora". Soon these predictions were shown to be true. Today, natural communities are experiencing a "convulsion" made up of over 480 000 species that have been intentionally or accidentally dispersed by man over the last 500 years outside their historical known native ranges (Pimentel *et al.* 2002). These human-mediated introductions of nonindigenous species, combined with habitat degradation, pollution and overexploitation, are dramatically leading to the "sixth extinction", an unprecedented loss of species occurring at rates of 100–1000 times those of past episodes of "natural" mass extinctions (Primack 1998).

Invasive species have come to dominate 3% of the Earth's ice-free surface (Mooney and Cleland 2001) and constitute one of the most serious ecological and economic threats of the new millennium (Cox 2004). Their negative effects to ecosystem health, indigenous species, economic interests, and public health have been well publicized in both the scientific and the popular literatures (e.g. Williamson 1996, Bright 1998, Devine 1999, Mack *et al.* 2000). They have been depicted as "agents of extinctions" (Lodge and Hill 1994), "components of global environmental changes" (Williamson and Fitter 1996) – perhaps even more significant than global warming (Daehler and Gordon 1997), causes of the "homogenization" (Lodge 1993) or "Mcdonaldization" of the biosphere (Lövei 1997), catalysts of global "McEcosystems" (Enserink 1999), and "ecological malignancies" (Gherardi 2000).

If this form of "biological pollution" is not stopped in time, it has been said that we will witness the formation of a "New Pangea" (Rosenzweig 2001), in which the indigenous species – the losers – will be replaced by a few winners – the invaders (McKinney and Lockwood 1999). Even intentional introductions, although made to provide benefits, may often result in a further case of the Frankenstein effect, i.e. attempts to improve nature may turn out to produce monsters (Moyle *et al.* 1986).

In spite of any preventative effort, the number of invasive species is expected to increase over the coming years (Ewell *et al.* 1999). In fact, the growth in volume and complexity of international trade has increased the frequency of species introduction along existing pathways, the number of new pathways, and the ease with which potentially invasive species can move along these pathways. Besides, the deregulation of national and international markets has reduced the barriers to trade and their surveillance. Human behaviour, social norms and cultural traditions have adapted only slowly to the new risks, and this, in turn, has increased the impacts of invasions (Perrings *et al.* 2002).

According to the majority of conservation biologists (e.g. Walker and Steffen 1997), the impact that invasive species exert on global biodiversity is second only to habitat destruction. Calls for more research to face the environmental crisis that they may cause are commonplace. However, when confronted with the quick disintegration of the "natural world", there are severe penalties for "fiddling" with ideas as long as one likes until the world is in ashes (Soulé 1986) –similar to the Emperor Nero who kept playing his lyre while Rome was burning. Often, the risks due to inaction may be greater than the risks presented by inappropriate actions and research appears "an unaffordable luxury that provides information only for the eulogy" (Coblentz 1990).

Yet, generalities are rapidly emerging in invasion biology, yielding encouraging insights into how invasions operate and how they may be best addressed by conservation managers and policy makers. Although complicated by economic, social and political concerns, invasive species policy decisions should be always based on clear and scientific reasoning (Byers *et al.* 2002).

I will raise here four questions about biological invaders and will outline the role of research in providing answers to those questions. Many examples will be taken from freshwater communities. Indeed, freshwater systems, whose value to humankind is obviously infinite, are particularly vulnerable to nonindigenous species due to both the strong affinity of humans for water (for commerce, transportation, recreation or aesthetic reasons) and the greater dispersal ability of freshwater species compared with terrestrial ones (Beisel 2001).

2. HOW TO DEFINE BIOINVADERS?

The importance of a uniform terminology in conservation biology is outlined by McShane (2003); "A confused semantics, he says, is the consequence of the increasing use – and abuse – of scientific terms and of their adoption by other spheres besides academia, such as conservation, law, media, politics, and science administration. Greater precision of these terms will be required to its users in such a way that policy and programs could be more efficiently defined in the future".

This is true also in the field of invasion biology. The attribute "nonindigenous" usually refers to a taxon (species, subspecies, race or variety, including gametes, propagules or part of an organism that might survive and subsequently reproduce; Scalera and Zaghi 2004) that has been introduced to areas beyond its native range by human activity, whether direct or indirect, intentional or unintentional. It is however subjective to set a threshold date of human introduction; most frequent thresholds have been set in either the Neolithic (i.e. 4000 BC; Manchester and Bullock 2000) or the 15th century (P. Genovesi – unpublished). Synonymies of nonindigenous include terms such as "adventive", "alien", "allochthonous", "exotic", "naturalized" and "non-native" (Occhipinti-Ambrogi and Galil 2004). Besides, the adopted terminology varies among scientific disciplines, linguistic and national borders, or is applied in different ways, and frequently is composed of synonyms and neologisms (Occhipinti-Ambrogi and Galil 2004).

Ironically, the greatest confusion surrounds the most common term "invasive" and its various derivatives (reviewed in Colautti and MacIsaac 2004); it lies among 1) a synonym of "nonindigenous", 2) an attribute of either nonindigenous species that are widespread or widespread nonindigenous species that have adverse effects on the invaded habitat, and 3) a component of a multi-staged process of invasion. Indeed, the co-occurrence in the literature of various definitions "may cloud theoretical issues, often leading to the lumping together of different phenomena and the splitting of similar ones, which in turn make generalization difficult or impossible" (Colautti and MacIsaac 2004).

The negative effects of a variegated terminology for management are magnified when definitions are used by the different actors of conservation. While the most widely accepted definition of bioinvaders in the scientific literature is "nonindigenous species that spread from the point of introduction and become abundant" (Kolar and Lodge 2001), the IUCN (2000) stigmatizes "invasive alien species" (IAS) as those species which "become established in natural or semi-natural ecosystems or habitats, are agents of change, and threaten native biological diversity". Similary, the Executive Order 13 112 (Clinton 1999) defines invasive species as those "alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health".

In these definitions of "invasive" and in most other similar definitions, "spread", "threaten", and "harm" are not determined quantitatively (Carlton 2002). Certainly, "invasive" is a powerful word conveying a sense of impact and urgency (Carlton 2001) but it is open to subjective assessments of negative consequences (Copp *et al.* 2005). In fact, any characterization that any or all indigenous species are good or bad is "a value judgment, not science" (Rosenzweig 2001).

Additionally, the attribute "invasive" does not divide species conveniently into taxa that have an impact and those that do not – invasions are not either "harmless" or "harmful". "The natural world – Carlton (2002) states – is a continuum of kaleidoscopic interactions, direct and indirect linkages, and intimately interwoven".

We should also remember that humans depend heavily on several nonindigenous organisms for food, shelter, medicine, ecosystem services, aesthetic enjoyment and cultural identity (Ewel *et al.* 1999). Over 70% of the world's food comes from nine crops (wheat, maize, rice, potato, barley, cassava, soybean, sugar, cane and oats) and 85% of industrial forestry plantations are established with species (*Eucalyptus*, *Pinus,* and *Tectona* spp.) which are cultivated far beyond their natural range. Although native organisms fulfill some human requirements, nonindigenous organisms play an integral role in the economies and cultures of all regions. Therefore, "the strongest ethical bases, and possibly the only ethical bases, for concern about introduced species are that they can threaten the existence of native species and communities and that they can cause staggering damage, reflected in economic terms, to human endeavors" (Simberloff 2003a).

3. WHAT IS THE ECOLOGICAL AND ECONOMIC IMPACT OF BIOINVADERS?

Biological invaders are commonly thought: 1) to alter and disrupt the biotic structure of ecosystems; 2) to affect the well-being of other species through competition, amensalism or swamping; 3) to push many species towards extinction; 4) to reduce the productivity of agriculture and aquaculture; and 5) to pose threats to human health and the health of domesticated or semi-domesticated plants and animals (Cox 2004). This latter point is well exemplified by the 1991 outbreak of cholera in Peru that caused the death of over 10 000 people, when ballast water containing the microbe *Vibrio cholerae* was released and infected drinking water (Bright 1998).

Obviously, our understanding of the threats posed by nonindigenous species is essential to sound environmental management. To prioritize management efforts, we should be able to rank nonindigenous species according to their impact in terms of modifications, alterations, and adjustments from a pre-existing state of the community prior to introduction (Parker *et al.* 1999). These changes range from small deviations to demonstrably very great ones, and may affect one or more pre-existing species. Similarly, societal (industrial, economic, social, recreational, health, and so on) impact may range vastly from low to medium and to high costs, with every nuance in between (Carlton 2002).

It seems obvious that experimental work is required to determine whether or not there is a statistically significant alteration in one or more parameters of the populations or communities of those species that existed at a given site prior to the introduction. Starting from the 1980s, research on the impacts of nonindigenous species expanded greatly, especially in North America, New Zealand, Australia, South Africa, and Western Europe, but it is still highly insufficient to address fully the threats posed by them. Conclusions about impact, or the lack thereof, are often based upon anecdotes and correlations, or, even less, on conjecture, suppositions, and presumptions (Carlton 2002). Especially in fresh water, attention has been directed to a few paradigmatic species on which knowledge is today extremely detailed. For instance, of the approximately 160 articles published between 1980 and 2005 on invasive freshwater molluscs, more than 75% have been devoted to the zebra mussel, *Dreissena polymorpha* (Pallas) (A. Ricciardi – unpublished). The large, wide-reaching effects of this mollusc on freshwater ecosystems are well documented (Strayer *et al.* 1999). Zebra mussel impacts multiple levels in aquatic systems, affecting in a direct and indirect way species composition, species interactions, community structure, and ecosystem properties (Karatayev *et al.* 1997, 2002, Strayer *et al.* 1999).

An unequal distribution of impact studies extends from the taxa investigated to the biological level analyzed, the individual and population levels being more extensively documented than the others. The most underestimated impacts are the genetic changes induced by nonindigenous species and the evolutionary effects following bioinvasions (Parker *et al.* 1999). The occurrence and consequences of hybridization between native and invasive species have been overlooked in most freshwater species except fish (e.g. mosquitofishes in North America, Courtenay and Stauffer 1984). It has been hypothesized that it was genetic assimilation that led about 38% of the North American extinct indigenous fish species to extinction (Cox 2004). The phenomenon of introgressive hybridization also seems to be frequent in crayfish. For instance, it has been documented between species of the crayfish genus *Orconectes*: matings between *Orconectes rusticus* (Girard) females and *Orconectes propinquus* (Girard) males yield a fecund and highly competitive progeny which is replacing the indigenous species in Trout Lake, Wisconsin (Perry *et al.* 2001). Other, subtler evolutionary changes (Cox 2004) may influence several life history characteristics of both invaders and indigenous species that are affected in a relatively short-time scale. Once established, nonindigenous species are freed from the constraints of gene flow from their parent population and from the biotic pressures of former enemies, are subject to altered selection pressures, and impose strong new evolutionary pressures on the natives. As an example, Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), native to the Pacific coast of North America, was introduced to New Zealand in 1901–1907. From the initial introduction, the species has colonized several river systems along the eastern coast of the South Island, giving rise to isolated populations. These populations now differ genetically among themselves and from their source population in California by several morphological and reproductive features, changes that have occurred in about 30 generations (Quinn *et al.* 2001).

Introgressive hybridization is only one of the several other mechanisms, includ-

Table 1. Percentages of native species in the United States threatened by various major impacts (from Wilcove *et al.* 1998). NIS denotes nonindigenous species.

	% of species affected by each factor				
Threatened species group	Habitat degradation and loss	Pollution	Over-exploitation	NIS	Disease
All species (1880 species)	85	24	17	49	3
All vertebrates (494 species)	92	46	27	47	8
Mammals (85 species)	89	19	47	27	8
Birds (98 species)	90	22	33	69	37
Amphibians (60 species)	87	47	17	27	0
Fishes (213 species)	97	90	15	17	0
All invertebrates (331 species)	87	45	23	27	0
Freshwater mussels (102 species)	97	90	15	17	0
Butterflies (33 species)	97	24	30	36	0
Plants (1055 species)	81	7	10	57	1

Species may be affected by more than one factor; therefore, rows do not total 100%.

ing parasitism, transmission of parasites, predation, competition for resources, and interference competition, that cause extinction, extirpation or endangerment of endemic species (Mack *et al.* 2000). Wilcove *et al.* (1998) judged that alien introductions were a significant factor in 47% vertebrates and 27% invertebrates that are now imperiled in the United States (Table 1). As far as fresh water is concerned, the North American fauna of mussels (the world's richest one, 296 species according to Perry *et al.* 2002) is particularly subject to risks. In fact, the zebra mussel and its close relative, the quagga mussel (*Dreissena bugensis* Andrusov), pose a serious threat to many species of the family Unionidae by fouling (i.e. by growing on unionid shells) or by competing for particulate foods (Strayer 1999). In Lake St. Clair all the native freshwater mussels were eliminated by 1997 after the appearance of zebra mussel in the early 1980s (Ricciardi *et al.* 1998, Nalepa *et al.* 2001).

Recently, Gurevitch and Padilla (2004) noted that declines of native species frequently overlap in space and time with invasions by alien species, and these co-occurrences are sometimes used to infer a causal relationship – a potentially erroneous conclusion given that a common factor, such as physical habitat alteration, might promote both extinction and invasion. Other causes may intervene to extirpate indigenous species, as shown also in one of the most celebrated extinctions, the extirpation from Lake Victoria of 200 of the 500 endemic cichlids by the Nile perch, *Lates nilotica* (L.), introduced in the early 1950s (Seehausen *et al.* 1997). The decline of cichlids started in fact in the 1920s with the development of railroads, erosion, and shoreline destruction. Then, the urbanization of the 1970s increased eutrophication and decreased lake transparency affecting sexual selection on cichlids; increased nutrients led to anoxic events and favoured the invader water hyacinth that may have altered nursery areas for juvenile fishes (reviewed in Gurevitch and Padilla 2004).

The story of the Nile perch exemplifies the difficulties encountered by researchers when they attempt to disentangle proximate and ultimate causes of native species extinction. It also underlines the need for a critical synthesis of data to assess the relative importance of invasions as a cause of extinction. Nonindigenous species might be, in fact, "a primary cause for decline, a contributing factor for a species already in serious trouble, the final nail in the coffin or merely the bouquet at the funeral" (Gurevitch and Padilla 2004).

Using the jargon of conservation economics, invasive species are externalities, that is "costs which a given activity unintentionally imposes on another, without the latter being able to exact a compensation for the damage received" (Perrings *et al.* 2000). However, external effects imply that, in order to persist, the damage must be associated with a continuing flow of output from the source. Bioinvasions, on the other hand, once set in motion are largely self-perpetuating. Even if the source of the introduction ceases its activity, damages from the invasives continue and often increase over time (Perrings *et al.* 2000).

Pimentel *et al.* (2005) provide an estimate of the yearly monetary cost of invasive species, including the direct damage and expenses for their control. In 2004, they amounted to 120 105 millions USD, a large portion of which came from the introduction of nonindigenous freshwater species (Table 2). However, if monetary values were assigned to species extinctions and losses in biodiversity, ecosystem services, and aesthetics, the costs of invasive species would undoubtedly be several times higher than 120 billion USD/year.

One of the few examples of costs associated with biodiversity loss in the freshwater domain comes from the Flathead catchment system in Montana, USA. The introduction, between 1968 and 1975, of the opossum shrimp, *Mysis relicta* Lovén, was aimed at increasing the growth of kokanee. On the contrary, it led to marked changes in the community. The density of two cladocerans, *Daphnia longiremis* (Sars) and *Leptodora kindtii* (Focke), decreased with the consequent crash of the population of kokanee that fed on the cladocerans rather than on *Mysis*. The abundance and diversity of birds and mammals, feeding on spawning kokanee, carcasses, and eggs, sharply declined. Among the others, the density of flagship species, such as bald eagles and grizzly bears, decreased. As a consequence, the number of tourists declined from 46 500 in 1983 to less than 1000 in 1989 causing an obvious economic loss for local activities based on ecotourism (Williamson 1996).

In a few instances, the deliberate introduction of invasive species into freshwater environments appeared to lead to revenues for local people. During 1975–1989, the introduction of the Nile perch into Lake Victoria was followed by 1) production gains amounting to about 280 million USD (at 1989 prices); 2) increased number of fishermen and of their dependents by 267 per cent (more than 1.2 million people depend today entirely on fishery); 3) ameliorated food quality for greater numbers of people; 4) intensified export that reached about 5–10% of the lake's production (Kasulo 2000). However, these estimates do not take into account the changes in the level and distribution of income, and in the ease of entry to the fishery trade. The new fishery has had the effect of concentrating income in the hands of a small minority of fishermen and the increased cost of boats and nets has been a barrier to ownership in the district (Kasulo 2000). Eventually, the Nile perch yielded an enormous indirect cost due to the extirpation of about 200 endemic cichlid species.

Table 2. Annual direct costs per millions of dollars in the US from invasive freshwater species compared with costs from diseases (Pimentel *et al.* 2004). Na denotes not available.

Category	Nonindigenous species	Losses and damages	Control costs	Total
Plants	25 000			
Aquatic weeds		10	100	110
Fish	138	5400	Na	5400
Molluscs	88			
Zebra mussel		-	-	1000
Asian clam		1000	Na	1000
Livestock diseases		14 000	Na	14 000
Human diseases		Na	7500	7500

4. HOW TO PREDICT POTENTIAL INVADERS?

Making predictions is an obvious priority for invasion biologists. If, on the one hand, learning to identify invaders in advance would tell us a great deal about how life history traits evolve and how biotic communities are assembled, on the other it might reveal the most effective means to prevent future invasions (Mack *et al.* 2000). Besides, preventing the introduction of potentially invasive species is the only environmentally sound approach to counteract the problems caused by invasions (Gollasch and Leppäkoski 1999). The stakes are extremely high, and it is far more difficult and expensive or even impossible to remove introduced species, once they are established, than first to keep them out.

Indeed, making predictions – the "Holy Grail of invasion biology" (Enserink 1999) – is extremely difficult. Unfortunately, only a few predictive models are available today and their application is restricted to a narrow range of organisms at best. On the contrary, the occurrence and timing of most invasions appear "as unpredictable as earthquakes" (Williamson 1999).

In the 1980s a flood of studies accompanied the rise in general awareness and concern around the invasive species problem. Today invasion biology, as a scientific discipline, has reached the phase of a "normal science" (Kuhn 1970). It is supported by a large body of theories and by robust methods of analysis. Notwithstanding that experimental data are still few (Kolar and Lodge 2001), patterns are emerging about the processes leading to both establishment of species outside their native range and their invasiveness. And all these are necessary prerequisites for predictions.

Now we know that invasions consist of several sequential transitions necessary for nonindigenous species to overcome dispersal barriers and move outside their native range (Fig. 1). To begin the invasion process, a species within its region of origin is carried by a transport pathway that deposits it outside its range. Today there is a fairly good understanding about the more likely vectors (Table 3). On the one hand, the 3–12 billion tons of ballast water transported by cargo vessels per year are thought to transfer 3000–4000 species per day from one continent to the other; by extrapolating these numbers to all the kinds of vessels at sea at any given time, we may estimate that about 10 000 species are transported per any 24 hour period (Carlton 1999). On the other hand, public or private mail and parcel post

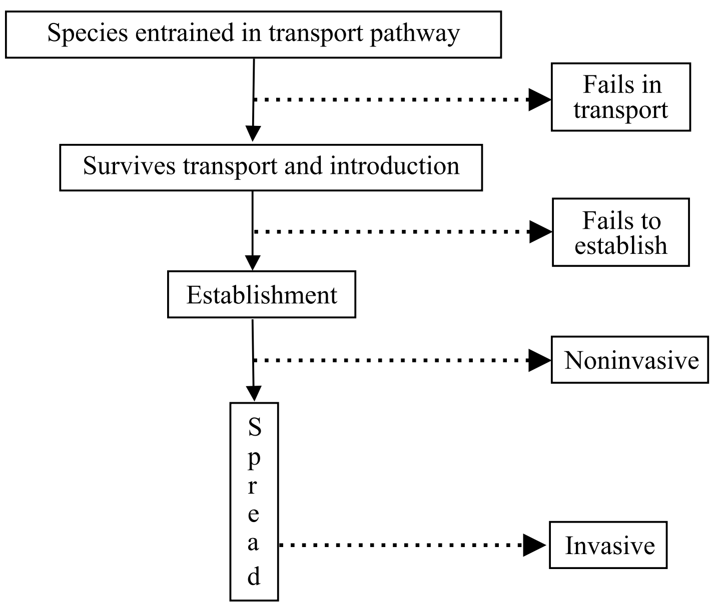

Fig. 1. Transitions that nonindigenous species must overcome to continue in the invasion process (Kolar and Lodge 2001).

Table 3. Main vectors of nonindigenous species.

1.	Ballast (both solid ballast and ballast water)
2.	Canal building providing corridors for rapid dispersal of aquatic organisms (e.g. the Welland Canal)
3.	Fouled ship hulls (also of recreational boats)
4.	Deliberate introductions of "desirable" species (for: agriculture/aquaculture, restocking, biocontrol or research)
5.	Deliberate releases of organisms not intended to form sustaining populations (unwanted pets or baits; parasites and disease agents from desirable species)
6.	Inadvertent release of organisms (escapes from aquaculture or agriculture, contaminants of deliberate release)
7.	The Internet trade

systems constitute a little-appreciated mode of dispersal of species, and the growth of e-commerce has thus increased this risk. Kay and Hoyle (2001), for example, found that almost every aquatic or wetland plant designed as a noxious weed could be ordered from an aquatic plant nursery somewhere.

Mathematical modelling and genetic studies have enabled detailed insights concerning both the geographic routes and the demography of invasions. For instance, they showed that the artificial canals linking naturally segregated catchments facilitated the diffusion of Ponto-Caspian taxa to the North and Baltic Seas, which was followed by a "jump" in ballast to the Laurentian Great Lakes (Cristescu *et al.* 2001, MacIsaac *et al.* 2001).

It is widely acknowledged that the successful establishment of an introduced species that results with the formation of self-sustaining populations is positively related to the "propagule pressure": invasion success increases with the number of propagules present in an inoculum and with the number of inocula (Williamson 1996). Although being intuitively obvious, its quantification is not of trivial importance with respect to prevention of nonindigenous species (Kolar and Lodge 2001). For example, accidental introductions of nonindigenous species via commerce-related activities, such as ballast-water release or movements of cargo containers, might be impossible to stop completely. Reducing the number of individuals released and the frequency of releases will, however, reduce the probability of establishment. However, predictions here are made more difficult by the "time lag effect" that acts as a confounding variable beneath establishment; in fact, it was shown that introduced species may stay at a low population size for years (0 for zebra mussels, 80 for the fungus *Entomophaga maimaiga* Humber, Shimazu et Soper) and then explode at some later date, usually following a logistic pattern of growth.

The literature on biological invasions is crowded with studies providing generalizations about traits that make species successful invaders (e.g. high fecundity, small body size, vegetative or asexual reproduction, high genetic diversity, high phenotypic plasticity, broad native range, abundance within native range, physiological tolerance, generalist habitat, human commensalisms) and habitats highly susceptible to invasions (climatically matched, disturbed, low diversity, absence of predators, presence of vacant niches, low connectance of food web). A number of theories have been proposed to explain why introduced organisms, once established in a new area, may become prevalent and spread. Among others, the "enemy release" hypothesis suggests that the reduced attack from natural enemies (predators and parasites) encountered by some species outside their natural range gives them the ability to spread and to become invasive. Torchin *et al.* (2003), for instance, showed that all the 26 invasive animal species they examined (from molluscs to rats) suffered from fewer parasites and pathogens in their naturalized than in their native range. Also, the impact of invaders should be most severe in communities lacking species similar to them, due to the community's lack of evolutionary experience with them (e.g. Diamond and Case 1986). For instance, by analyzing several aquatic systems from the Laurentian Great Lakes to the New Zealand coast, Ricciardi and Atkinson (2004) showed that the magnitude of an invader's impact is related to the invader's "taxonomic distinctiveness" within the recipient community. Often, the colonization by nonindigenous species facilitates, rather than interferes with, the establishment of other nonindigenous species and/or their continued existence, and therefore increases the likelihood and the magnitude of ecological impact as suggested by the "invasional meltdown theory" (Simberloff and Von Holle 1999). Finally, indigenous species-poor communities and/or ecosystems with elevated niche opportunities were shown to be more vulnerable to invasions (e.g. Levine and D'Antonio 1999, Shea and Chesson 2002).

Often, the "tens rule" (Williamson 1996) has been invoked to predict the relative number of introduced species that overcome the several barriers encountered in the recipient ecosystem and become invasive. This rule-of-thumb estimated that 10% (between 5% and 20%) of introduced species become established, and, on average, 10% of those established become invasive. But this rule provides only a rough guideline. Recently, Jerscke and Strayer (2005) questioned the tens rule, showing that in several taxa, especially in vertebrates, establishment and spreading success far exceed 10%. They also showed the critical importance of the first step of the invasion process, introduction. Vertebrates have by far the lowest success in taking this step, so the most effective control of their invasion is to prevent them from entering a new range. Once introduced, vertebrates have a high potential to establish and spread.

Although progress has been made in predicting ongoing bioinvasions, it is desirable that most research effort be soon directed to estimate impacts from species before their introduction and therefore to develop reliable protocols for risk assessment of species importation, as recommended by the Convention on Biological Diversity (CBD 2001). Lack of precision should not be viewed as a deterrent to making predictive models where none exist. Even crude models (constructed from reliable data) have potential value and can be refined as additional data become available (Ricciardi 2003). They might also help natural resource managers to reduce the occurrence and impact of nonindigenous species and guide the efficient allocation of management and policy efforts towards the most invasive species.

Finally, attention should be directed to the final stage of invasion, sometimes described as "integration". This is a process in which the species in the recipient community and the invaders respond to each other ecologically and evolutionarily (Vermeij 1996). The invaders, by affecting abundances of the indigenous species, may modify the agencies of selection on those species and, by establishing interactions with hosts and parasites, may be themselves subject to new population controls and selective regimes. In the light of these outcomes, researchers should ask whether the ecological changes induced by invaders are reversible, and whether the elimination of the invasive species necessarily brings the recipient community to the conditions before invasion (Vermeij 1996).

5. HOW TO MANAGE INVADERS?

The role that science plays in facing ongoing invasions has been recently questioned by Simberloff (2003b). There is no doubt, he says, that scientific research yields major insights into areas of ecology, evolution, and conservation biology. The frequent presence of serendipity in science (i.e. the faculty or phenomenon of finding valuable or agreeable things not sought for) ensures that some fraction of these insights will ultimately aid management. But most of them will have "little direct relevance to the introduced species problem" (Simberloff 2003b). On the contrary, by acting quickly without much biological knowledge, we can save a huge amount of trouble and costs, and avoid uncertain prospects for successful subsequent management. A "quick and dirty" response, mechanical or chemical or both, often solves the problem at the outset by eliminating the invader.

The invasion story of the tropical marine alga *Caulerpa taxifolia* (Vahl) in the Mediterranean (Meinesz 1999) exemplifies the damage caused by a slow response. *Caulerpa* was first observed in a tiny area in front of the Oceanographic Museum of Monaco in 1984 and would have been eradicated soon simply by hand-removal. But the intervention was delayed for years, partly because of academic controversy, partly because of unclear distribution of roles (Genovesi 2005). As a result, the alga now infests several thousand hectares of the coasts of Spain, France, Monaco, Italy, Croatia, and Tunisia.

Often, successful eradication and control measures did not require extensive population biological research. Two pairs of the Canadian beaver, *Castor canadensis* Kuhl, escaped from a park in the St. Fargeau area (France) and established in a river in 1977. In 1984–1985, the population, composed of 24 individuals, was eradicated without any research (Rouland 1985). The water hyacinth *Eichhornia crassipes* (Mart.) arrived in Florida in the early 1880s as a horticultural curiosity and was rapidly spread by farmers as cattle food. By the end of the nineteenth century it became a pest (Schardt 1997). Many techniques were tried to control it without success. Starting from the 1970s, the use of mechanical harvesters and the herbicide 2,4-D quickly reduced the coverage from 50 000 to less than 1000 ha and every year small infestations are destroyed with a cost of approximately 2.7 million USD per year.

There are, however, also success stories in fresh water where invasions were not detected early but were nevertheless eradicated because long-term studies on population ecology enabled researchers to predict the outcome of the adopted strategy. The eradication of the coypu from East Anglia (England) in 1981–1989 is a clear example of a situation in which a strategic plan was an essential part of the intervention (Gosling and Baker 1989). It succeeded largely because of the investment in research on applied population biology and ecology, which was vital in planning and guiding the campaign. Research included studies of alternative control strategies and forecasted how long the campaign would take and how much it would cost. Biologists guided and monitored the progress of the campaign and designed the criteria for judging when it should end (Gosling 1989).

6. CONCLUSIONS

Any attempt to manage the invasive species problem will greatly benefit from a constructive partnership between researchers and conservation managers (Byers *et al.* 2002). Specifically, the progress of any form of adaptive management (Walters and Holling 1990) will be hastened by direct scientific feedback. Researchers are required to identify and control pathways of accidental introductions, to promote measures to prevent unwanted introductions, and to produce protocols for pre-introduction environmental risk assessment. They should stimulate cooperative actions among States, recognising the risk, particularly high in Europe, that activities within their jurisdiction or control may pose to other States as a potential source of invasive species. By quantifying how invasive species affect native biodiversity, scientists should also assess the environmental costs associated with different control strategies and with immediate, delayed, or absent reaction to the presence of nonindigenous species.

Research is also needed to indicate control/eradication methods of invasive species, methods which should share the attributes of being the most efficient, non-polluting, and not risky to native flora and fauna, humans, domestic animals, and cultivars. Researchers have the potential to determine metrics that could reflect all the biological, as well as social, economic, aesthetic changes that accompany the intervention. They should evaluate the role of nonindigenous species after their integration in the systems, recognize that a return to the pristine state is often impossible, and suggest strategies that are flexible and in line with biogeographic and evolutionary realities (Cox 2004). Finally, research will help prioritize ecosystems at risk through assessing their invasibility and the duration of lag phases between the establishment and spread of specific invaders.

Given all this, researchers will easily solve the Nero dilemma. In designing experimental studies on invasive species, they should be fully aware of their role in the “real world" outside the academy, be ready to face the critical challenges addressed by conservation managers, and be willing to interact with them.

ACKNOWLEDGMENTS: Warm thanks are directed to Prof. Maciej Gliwicz and to the organizing committee of the Symposium for European Freshwater Sciences in Krakow for their kind hospitality and constant help.

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(Received after revising December 2005)